

Recent *Poritidæ*, and the Position of the Family in the Madreporarian System. By HENRY M. BERNARD, M.A., F.L.S.

[Read 2nd February, 1899.]

IN the last paper dealing with the Stony Corals which I had the honour of reading before this Society *, a phylogeny of the Madreporarian skeleton was sketched out, and suggestions were made as to the lines of development which had been taken by some of the better-known recent forms. I now propose to give an instalment of the morphological results of work done during the past eighteen months on one of the families mentioned in that paper—the *Poritidæ*. It is hoped that in the course of the next few years the remaining groups of the Madreporaria, both recent and fossil, will be dealt with, and the proposed phylogenetic scheme completed and strengthened by additions and amendments suggested in the course of the work.

In this paper I propose to confine myself to the systematic position of the *Poritidæ*, and to introduce only so much structural detail as is necessary. The variations of form assumed by *Porites*, a few of which are only incidentally referred to here, deserve separate description. The most important question raised by the work itself, however, was primarily the place of the *Poritidæ* among the Madreporaria. This point has therefore been worked out first, and the present paper will be shortly followed by a more detailed account of the structure and of the chief lines of differentiation found within the constituent genera.

But, while reserving an account of the structure for fuller treatment in a second paper, a brief description of the corals known as *Porites* will doubtless add to the interest of the following pages. Although both explanate and branching forms are known, the most familiar are smooth round masses, sometimes attaining a circumference of 60 feet. They are built up by a dense crowd of minute cylindrical polyps characterized by twelve short, thick, (?) rudimentary tentacles. The polyps rise fairly high above their skeletal substratum, and when retracted are unable to withdraw entirely into their calicles, as is the usual habit in the Stony Corals. Examination of the dried skeleton shows that the pits are too shallow to take in the polyps; they

* Journ. Linn. Soc., Zool. xxvi., read December 1897.

are, in fact, little more than surface depressions in a skeletal mass, conspicuous on account of its being a fine porous reticulum. The shallow calicles may be rounded and separated by reticular walls of different thicknesses, or else so crowded together as to be polygonal in outline. The skeletal structure within the calicle is also remarkable. The radial symmetry, which is such a striking feature in the Stony Corals, is in *Porites* more or less obscured. Septa never stand out as radiating plates, but instead 5-6 or more red-like or granular pali rise up as a central ring from the reticulum which fills up the base of the calicle. Round this ring of pali the rudiments of septal formation can generally be traced.

Such corals as these early attracted the attention of naturalists, and the significant name *Porites* was first associated with them by Pallas (1766), and was eventually accepted by Lamarck as the generic name.

The position which Lamarck assigned to the new genus is given in his classification of the "Lamelliferous" Corals (*Anim. s. Vert.*, ed. 1816, ii. p. 219). It is placed with *Madrepora* in the last section, viz., in that which contained corals with cells circumscribed and covering the whole free surface of the stock, and it follows *Astræa*, which also has cells circumscribed but confined to the upper surface of the stock.

In 1821* Lamouroux followed Lamarck in placing the genus *Porites* after *Astræa*, but called the group in which the former occurred "Les Madréporées," and that in which *Astræa* occurred "Les Astrées." De Blainville † divided the Stony Corals into "Madrephyllies" and "Madrepores," the Astræids being placed among the former and *Porites* near the end of the latter. Nevertheless, in his observations he admits the apparent kinship of the genus with both *Astræa* and *Madrepora* as suggested by Lamarck, but thought it was much closer with the latter than with the former. The recently established genus *Goniopora*, Q. & G., was rightly placed by De Blainville next to, but in front of, *Porites*.

In 1834 Ehrenberg ‡ placed *Porites* in the "Madreporina," which were quite distinct from the "Astræina." The Madreporina were divided mainly according to their methods of

* 'Exposition Méthodique,' pp. 56, 60.

† 'Manuel,' pp. 334, 395.

‡ 'Corallenthiere des Rothen Meeres,' pp. 91-115.

budding into two genera, *Heteropora* (= the modern genus *Madrepora*) and *Madrepora*, Ehr. This latter consisted of two subgenera, *Madrepora-phyllopora* (= *Astræopora*, de Biv.) and *Madrepora-porites*, which was a heterogeneous group consisting of Montipores, Stylophores, Alveopores, with a few true Poritids.

Dana* was the first to found the family Poritidæ, of equal value with and closely allied to the family Madreporidæ. It contained two genera, *Porites* and *Goniopora*.

This arrangement of Dana's was, in the main, accepted by Milne-Edwards and Haime in 1851. The Poritidæ, enlarged by the addition of many more genera, constituted, together with a very large family the Madreporidæ, the great section Madreporaria Perforata, as opposed to the greater bulk of the remaining Stony Corals, which were grouped as Madreporaria Aporosa. This recognition of the structure of the coral-skeleton as a feature of fundamental taxonomic importance is the chief merit of the work of these authors, which is the last comprehensive attempt to classify the whole coral system. It was, however, hardly to be expected that this first attempt to solve the difficult morphological problems presented by the coral-skeleton would be successful. It is not, therefore, surprising to find that every advance in our knowledge of corals has led to some sweeping revision of Milne-Edwards and Haime's system. At the present day only two of its five original sections can be said to have held their own, viz., the two most important, the Madreporaria Aporosa and M. Perforata †. That these two are now in their turn on the eve of modification, the extent of which cannot yet be predicted, because the researches which render revision necessary are still too recent, will, it is hoped, be made clear in the following pages. Criticisms of details have not been wanting, but they have mainly referred to the relative positions of families or genera.

No change has, so far, been made affecting the position of the Poritidæ, which is the matter we have especially in hand in this paper. The only expressed doubt as to their affinity with the Madreporidæ with which I am acquainted is in the recent work of Miss Ogilvie ‡, who found it impossible to decide whether the two families were or were not related.

* 'Zoophytes,' 1848.

† See Martin Duncan's revision of the system in the Journ. Linn. Soc., Zool. xviii. 1884, p. 3.

‡ Phil. Trans. vol. 187, 1896, p. 327.

This brief historical sketch shows that almost all who have studied the Madreporaria have come to the conclusion that *Porites* is in some way related to the Madreporids. The reasons for this conclusion may be briefly arranged under the following heads:—

1. The general similarity of their polyps, with twelve tentacles in a single ring.
2. The fact that the septa are mostly in some low multiple of six. In *Porites* there are almost invariably twelve.
3. The skeletal walls are porous, and in both tend to form reticular cœnenchymas*.

Although the real value of this last point, viz., the possession of porous or reticular walls, has never till recently been understood, it was nevertheless a common character in striking contrast with the solid mural structures found in the Astræidæ.

As opposed to these common characters uniting the two families, we have certain differences keeping them apart. These were described by Dana, who limited the family to two genera, *Porites* and *Goniopora*, as follows:—(1) Extraordinary porosity of the Poritid skeleton as compared with the more regularly lamellate skeleton of the Madreporidæ; (2) the fact that, in the Poritidæ, the skeleton in its relation to the polyp is purely basal and never rises to a deep cup; (3) that, as it grows, the small central depression of the calicle fills up, so that the stars are hardly or not at all traceable through the substance of the corallum, as they always are in the Madreporidæ.

On the other hand, Milne-Edwards and Haime, carried along by their theory of the origin of the Madreporarian skeleton, believed that the "trabecular" character of the septa in *Porites* was the fundamental distinction, the septa in the Madreporidæ being lamellate. The remaining differences above quoted from Dana were no longer applicable, because several other genera with the so-called "trabecular" septa were now included.

As it is useless to attempt to discuss these resemblances and differences until we understand clearly what is meant by the terms used, it is necessary to sketch the fundamental theory

* Milne-Edwards and Haime also added that the families agreed in having no tabulæ, which are so common in the Astræids. This distinction is incorrect. I have already described tabulæ in *Astræopora* and *Turbinaria*, and find them also in *Goniopora* and specially numerous in *Porites*.

upon which the system of Milne-Edwards and Haime was based. It must be remembered that this system, though 50 years old, has never yet been superseded so far as the two chief divisions of the Stony Corals are concerned, the perforate and imperforate. Though worker after worker finds it obsolete, no comprehensive criticism of it has yet been attempted in connection with systematic work*. I make no excuse, therefore, for reviewing the situation which recent researches have brought about. If I needed any excuse I should find it in the great trouble and perplexity which the word "trabecular" has caused me during the past few years. The reason of the confusion can best be explained by showing with what total absence of precision the term was originally used. I hope to make this quite clear by means of concrete examples.

According to Milne-Edwards and Haime the Madreporarian skeleton was built up by the fusion of vast numbers of spicules like those found isolated in the Aleyonaria. Fusion by terminal growth of isolated spicules would naturally result in a reticulate corallum. Direct evidence of this theory was found in the fact that Madreporaria still existed in which the skeleton was reticular, the septa being a lattice-work. *Porites* showed these primitive skeletal conditions best, but others, e. g. *Goniopora*, *Alveopora*, and *Montipora*, were all sufficiently reticular, or, as it was called, "trabecular" †, to be united with *Porites* in one family. Corals showing a further degree of fusion were the Madreporidæ, in which the septa are for the most part lamellate, and only the walls are reticular. Thus the Poritidæ and the Madreporidæ were classed as Perforata in contrast to those corals, such as the Austraids, which showed a still higher degree of specialization, both septa and walls being solid throughout.

It is needless to criticize the details of this scheme, since it has been recently proved to rest upon an entirely erroneous conception of the origin of the Madreporarian skeleton. We now know, primarily through the researches of Dr. von Koch, that the Madreporarian skeleton is a purely ectodermal secretion, and that the septa which appear to be internal are always clothed

* The bearing of Miss Ogilvie's work will be alluded to in the course of what follows.

† For criticisms of this term see pp. 137 & 145.

with a layer of ectoderm-cells. The whole skeleton is thus outside the polyp, and could never have been built up by a fusion of spicules developed inside the body.

With regard to the general bearing of Dr. von Koch's discovery on the origin and classification of the Madreporaria, I venture to believe that the phylogenetic scheme which was presented in my last paper to this Society supplies us with a solid foundation on which to build up a natural system. That this scheme was only partially seen by Dr. von Koch himself is not to be wondered at; the clue to it lay hid entirely in the epitheca, the great importance of which seems everywhere to have escaped attention. Dr. v. Koch's conclusion was that the "basal plate" with the "epitheca" (that term being commonly limited to the continuation of the basal plate a short way up the sides of the polyp) together formed the primitive skeletal cup of the Madreporaria*.

This description, though correct in fact, fails to recognize the fundamental morphological importance of the epitheca. My own systematic studies had, on the other hand, led me, along quite independent lines, to the conclusion that the epitheca, from which it is impossible to separate the basal plate as a distinct morphological unit, had been at one time the most important element in the skeleton, and that, though it is now very generally vestigial, it was the original cup-like exoskeleton of the Stony Corals from which all the later internal (septal) skeletons had been developed by infoldings. This view is fully supported by the facts:— (1) That the epitheca forms such cup-like exoskeletons in the earliest stages of many (? all) Stony Corals; (2) that transitional forms such as *Alveopora* occur, in which the primitive importance of the epitheca is much longer retained; (3) that many Palæozoic corals are almost purely epithecate; and (4) that published drawings of sections of *Flabellum* show the septa as if they were still formed as simple infoldings of an external wall †.

This was summed up in my previous paper (*l. c.* p. 514) in the following words:—"The Madreporarian skeleton may be described as the rigid secretion of the basal portion of the columniform body of a polyp into which the flexible upper portion may

* Gegenbaur's Festschrift, ii. 1896, p. 272.

† *Cf.* p. 134.

be invaginated. In its earliest development a simple cup, it has become complicated in various ways; primarily, by the development of radial infoldings of the stiff external wall, comparable with the infoldings of the chitinous cuticle of Arthropods: secondarily, (1) by further complications of these infoldings so as to form an intricate 'internal' skeleton, which may render the primitive external cup unnecessary, and hence lead to its becoming vestigial; (2) by a process of repeated sheddings of the external hard secretions, and the formation of new ones (dissepiments and tabulæ) across and among the existing 'internal' skeletal structures."

Further work with Madreporarian skeletons has only confirmed this generalization. One or two points, however, require attention. In my former paper these septal infoldings were likened to the apodemes of Arthropods, formed by the infoldings of the chitinous skeleton which sometimes, *e. g.* in the cephalothorax of the Spiders, form together an elaborate internal framework. While this resemblance is structurally accurate, the comparison must be received with caution. The apodematous system of the Arthropods can be shown, even in detail*, to be due, at least in their earliest stages, to muscular action, either directly drawing in the chitin to which it is attached, or causing deep wrinkles or folds across the line of the muscles. But it is difficult to see how the infoldings of the calcareous exoskeleton of the early Madreporæ to form septa could have been due to muscular action. Dr. von Koch (*l. c.*) thinks that the septa might have arisen in connection with certain endodermal ridges found in some larvæ. But we shall be probably nearer the truth if we can find a cause for them in the ectoderm itself. Until recently I thought that they were due to increased local activity in the secretion of calcareous matter, which would therefore push in the body-wall. From this point of view I found fault (*Geol. Mag.* 1897) with Miss Ogilvie's description of the process as an "invagination which became filled up" with skeletal matter. But this terminology, though not felicitous, need not be altogether wrong. It seems to me not unlikely that the puckering which gave rise to the septa was caused by the growth of the basal, and probably best nourished, wall of the polyp, and that this wall, cramped by the primitive exoskeletal epitheca, could

* *Ann. & Mag. Nat. Hist.* (6) x. p. 67 (1892).

only increase by the formation of folds. We can well understand how such puckering might be radial in the bases of the mesenterial chambers, but quite irregular in the base of the central cavity, where the radial puckers would meet and fuse together with twists and curves. Under the radial puckers, the ectoderm would secrete the septa; under the central, the columella. This view finds some support in the fact that fresh septa are added by puckering of the ectoderm just below the rim of the epitheca (or subsequently of the theca) of the growing coral, *i. e.* just where the polyp is trying to expand*.

Again, in endeavouring to establish my argument that the septa arose from infoldings of the epitheca, I appealed to sections of *Flabellum*. While this appeal is, I think, perfectly justifiable, the sections demonstrating in a remarkable way the point it was desired to establish, yet I confess that, at the time, I did not see that this case itself (*Flabellum*) required explanation. For such direct infoldings of the epitheca from the external surface cannot be considered as primitive. As far as we can see, the epitheca must primitively have formed a continuous calcareous layer, and, when infoldings began, they must have risen from its inner surface without the possibility of there being any external scar such as necessarily exists in the case of chitinous infoldings in the Arthropods, at least until secondarily obliterated. The direct infoldings of the epitheca of *Flabellum* with external scars are therefore somewhat startling. Dr. Ortmann's sections of *Flabellum*, it is true, show an external layer but with a circumferential dark line †, indicating that this layer itself was formed under a fold. I have already suggested that this discrepancy between Dr. Ortmann's sections and those of Dr. Fowler, Mr. G. C. Bourne, and Dr. von Koch can be explained by supposing that, in the case of his specimens, there had been a bagging of the soft parts over the rim of the epitheca which would cause it to grow as a fold. That some specimens do thus bag over we know from Moseley's account of *Flabellum* (Chall. Rep. ii. p. 162, 1881). But this folded rim is not exactly what is wanted. We should have expected a simple rim of epitheca without any dark

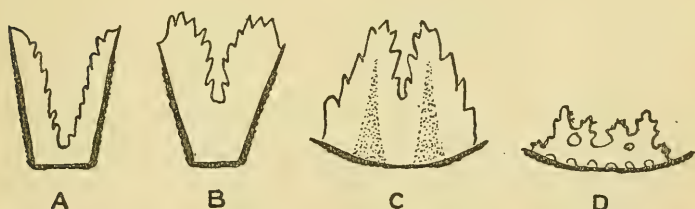
* In my former paper I described other results of this effort to grow, viz. the bagging of the polyp or even its overflowing over the rim of the epithelial cup.

† Zool. Jahrb. iv. (Syst.), pl. xviii. fig. 9 (1889).

line outside the first beginnings of the septa. The fact that this is not found—*cf.*, *e. g.*, Dr. Fowler's sections (Q. J. M. S. xxviii.)—required explanation; and that probably lies in the fact that the puckering of the expanding ectoderm in the early stages of the epithelial cup extends beyond its rim, and that consequently, when this puckered skin secretes its exoskeleton, the latter is puckered or folded from the first.

The last matter to which I wish to refer is still more important, and, moreover, it brings us back to the main subject of our paper, *viz.*, the affinities of *Porites*. One of the special difficulties in dealing with the morphology of the Madreporaria lies in the fact that, for precision's sake, we have to idealize the parent polyp and picture to ourselves the possible transformations of its skeleton, as if it remained stationary. But, as a matter of fact, budding and colony-formation come in to complicate matters greatly. This, therefore, we must face as a difficulty in the way

Fig. 1.



A and B. Epithecal stages; the septa developed in A, become exsert in B.
 C. Thecate stage; the exsert septa replace the epitheca, which becomes vestigial. D. Diagrammatic section of *Porites*.

of our line of argument. We have, for instance, assumed that the epithelial cup became vestigial because it was rendered unnecessary by the rising up of the septa (fig. 1) above the edge of the epithelial cup to form an internal theca, which supplied in every way a stronger and better-defended retreat for the polyp than the epithelial cup itself with its edges tending to be filmy and friable. Now, while a comparative study of the different forms of calicle leads me to believe that this is actually what took place, yet, when the habit of budding and colony-formation is taken into account, we are forced to ask whether a reason for the degeneration of the epitheca might not also be found some-

where in this latter. That such may indeed have been the case we know from the fact that species of *Alveopora* occur in which the lateral expansion of the colony is so pronounced that the usually conspicuous epitheca becomes little more than a film protecting the coral from the substratum, although there are here no exsert septa out of which to form an internal theca in the manner shown in the diagram. The same can also be shown in the genus *Goniastrea*, which multiplies by what is called fissiparity. Two prominent septa mark off the skeleton of the bud*. The skeleton of the colony is here again septate, and the epitheca is flattened out by colony-formation, that is, not in the way shown in the diagram.

This point was not evident in my former paper, even though I left it undecided whether *Porites* was to be regarded as related to Madreporidæ or to *Alveopora*. It was quite clear that the epitheca of *Porites* was flattened out, and that the theca was therefore internal (fig. 1, D); but I saw only two ways in which this could have occurred, and in both the epitheca was slowly replaced in an essentially similar way, viz., by the rising up of an internal theca, formed by the septa becoming more and more exsert. The theca of *Porites* might, I thought, be either a secondary modification of that of the Madreporidæ by the perforation of the lamellate septa, or an independent development from a form like *Alveopora* with horizontal spine-like septa. In this latter case, as the epitheca flattened out, the spines would become vertical and form the vertical "trabeculæ" of *Porites*. I now see, however, that the epitheca might be flattened out in the process of colony-formation, when the skeleton of the bud is marked off by the meeting of septa which cut off a portion of the parent calicle.

We have, then, three apparently possible origins of *Porites*. Of these we may, I think, safely dismiss this last supposition, viz., that the flattening out of the epitheca was due to the rapid lateral budding of some fissiparous coral. Such an origin would give us no explanation of the radial series of "trabeculæ" or of the thick intervening walls.

Returning, then, to the main alternatives, we have to decide

* This method of budding may be compared with that described in a former paper (Journ. Linn. Soc., Zool. vol. xxvi. p. 495, pl. 33. fig. 10) as that of an Astræid!

whether the internal theca of *Porites* has been developed out of the exsert septal spines of a Favositid, or is a secondary modification of that of the Madreporidæ, with its ring of lamellated septa.

Recent work with both *Goniopora* and *Porites* has led me to the conclusion that this latter view is the correct one. *The septa in both these two genera were once purely lamellate.* Proof of this can be seen in the fact that, both in *Porites* and in *Goniopora*, every transition can be found between the forms with almost purely lamellate septa and others with purely "trabecular" septa. Further, in a great many forms, the costæ round the growing edges run out as vertical lamellæ to the rim of the epitheca, that is, just where primitive conditions might be expected.

This conclusion is not only of permanent importance for the solution of the problem we have in hand, but it deserves the special attention of all students of Stony Corals, because it relieves them for ever of the "trabecula" as a unit of morphological value. The "trabecula," which is in reality merely so much formative tissue, was brought into the system by the theoretical scheme of Madreporarian tectonics put forward by Milne-Edwards and Haime, a scheme which Miss Ogilvie * has recently endeavoured, by considerable emendation and amplification, to place on the surer basis of extended histological research. How great a snare it has been I have already shown † in the case of *Montipora*, which, on account of its "trabeculæ," was ranked by Milne-Edwards and Haime among the Poritidæ. The "trabeculæ" of *Montipora*, that is, if what I called the trabeculæ of that genus are what Milne-Edwards meant, turned out on examination to be very different from those of *Porites* (see further on this point below). Again, if the trabeculæ in *Porites* and *Goniopora*, in which genera of all others they appear to play the most important part, can yet be shown to have no real morphological value, their case finally breaks down.

My own experience is as follows. I began work first with *Goniopora*, its larger calicles admitting of easier examination. At the outset the "trabecula" was accepted as a morphological

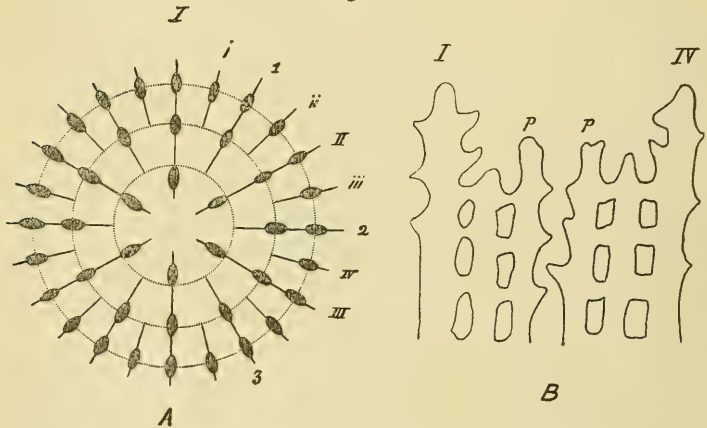
* Phil. Trans. vol. 187, 1896.

† Ann. & Mag. Nat. Hist. xx. 1897.

unit. The following reasons seemed to justify this acceptance:— (1) Well-developed “trabeculæ” occur in the walls of many species. (2) The pali appear to be the tips of others. (3) A vertical section through a corallum frequently shows it to have been built up of long nodulated threads (trabeculæ) running in the line of growth and joined together at intervals by cross-pieces arranged parallel with the surface: this, however, is truer of *Porites* than of *Goniopora*. (4) In some forms there appeared to be a regularity in position and arrangement of the trabeculæ which suggested their having real value.

After examining a great number of specimens, I reconstructed on the simplest possible plan an ideal primitive skeleton of a Goniopore built up of trabeculæ (see fig. 2). But the longer the actual specimens were studied with this hypothetical ancestral

Fig. 2.



Ideal arrangement of the “trabeculæ,” if regarded as morphological units, necessary to explain the skeleton of a Goniopore, the columellar tangle being omitted. A, in ground plan: B, in vertical section; *p*, central pali.

form, the more impossible it became. The meshes of the lattice-work were always pores, often very irregular in size and arrangement, in otherwise lamellate septa. Surely some forms would have retained the rectangular lattice-work with the trabeculæ persisting in their primitive importance. But no such condition was found. Then, again, the pali failed as tips of growing trabeculæ. They were plates when the septa were but slightly perforated, and were only tips to the narrow divisions between the large perforations in other cases. Lastly, the finding of the growing

edges, already mentioned, in which lamellate costæ ran out to the rim of the epitheca, finally convinced me that the so-called "trabecular" septa are merely perforate lamellate septa.

We have thus reached an important stage in our enquiry as to the position of the Poritidæ: their so-called "trabecular" structure belongs to the terminology of the past. Their thecæ were originally built up of lamellate plates like those of the Madreporids, and the perforation of these plates has to be considered as a secondary characteristic. To this difference between the Madreporid and the Poritid septum we shall return when we have discussed the next most striking contrast between the two families, which may be stated as follows:—

In the Madreporidæ, except in *Montipora* with its immense development of the cœnenchyma, the thecæ are tall and conical. In the Poritidæ, on the contrary, the thecæ are low and shallow. The septa in the latter are therefore not only perforated, *i. e.* poor in quality, but also poor in quantity, that is in size.

This contrast is shown diagrammatically in fig. 1, p. 135, in which C and D are intended to represent individual calicles (ideal parent calicles) of a Madreporid and of a *Porites* respectively. In the former, the septa rise above the flattened epitheca to form a new theca, being mutually supported by synapticulæ which would project from the plane of the figure in the dotted areas. In the latter we have the low basal skeleton of *Porites*; the septa with their synapticulæ being together reduced to a reticulum. Can any explanation be given of these differences? I think so. The diagrams of themselves seem to suggest that the conditions found in *Porites* are due to arrested development. The suggestion is therefore made that these swarms of minute polyps, which are so ubiquitous and appear in such vast numbers that they are reckoned among the principal builders of the coral-reefs, may be regarded as Madreporids arrested at an early stage in their development. This is, in fact, the position I have found myself compelled to assign to the Poritidæ in the Catalogue of the British Museum Madreporaria*.

* Vol. I. (by the late George Brook) deals with *Madrepora*. Vols. II. & III. contain the Madreporid genera *Turbinaria*, *Astræopora*, *Montipora*, and *Anæcropora*. Vol. IV., which is nearing completion, contains the two Poritid genera *Porites* and *Goniopora*, somewhat extended (see below, pp. 143-148).

Let us then see what are the arguments in favour of this suggestion. For the moment, dealing only with *Porites*, we find the polyps, like their calicles, small and degenerate, *i. e.* little grown and with only twelve tentacles. Their skeletal secretions are purely basal, and the animals retreat down upon them rather than into them*. Thus, in relation to the animal, the skeleton is but feebly developed, so feebly indeed that the coralla rarely have any elasticity or beauty of form. They are, for the most part, merely rounded massive concretions such as could be built up of small flat discs.

It may perhaps be objected that such a poorly developed and rudimentary skeleton might also be primitive, but this is certainly not the case here; for a glance at fig. 1 shows that the skeleton of *Porites* belongs to the highest known type, viz., that in which an internal theca has replaced the primitive epithecal cup. This, as above stated, I believe it could only have done by the internal theca being pronounced enough to replace the epithecal cup as a more efficient refuge into which the polyp could contract. Hence we can only account for the internal theca of *Porites* by assuming that it was at one time tall and deep, forming with its jagged septal edges a stronger and better guarded receptacle for the polyp than the primitive epitheca. In other words, the theca of *Porites* must at one time have been tall and composed of lamellate septa, and the fossa, now shallow and quite incapable of containing the polyp, must at one time have been large enough to have allowed the whole polyp to sink down into its recesses (fossa, interseptal and intercostal spaces). The theca, from being a true calicle, has become, in *Porites*, a mere basal pedestal for the comparatively speaking tall polyp which secretes it, it being one of the peculiarities of *Porites* (and of *Goniopora*) for the polyps to rise high above their skeletons.

The internal theca of *Porites* can therefore only be regarded as rudimentary. It is not a vanishing structure, but it belongs to the most specialized type of Madreporarian skeleton, secondarily arrested in its development. This interpretation is further confirmed by comparing the skeleton of *Porites* with that of almost any minute young single coral, such as is frequently found

* Thurston describes the polyps of *Porites* which can no longer retreat into their calicles as protecting themselves when exposed by a layer of slime. Bulletin of Madras Government Museum, No. 3 (1895), p. 93.

on the corroded bases of large stocks. The septa of such young forms are seen to be irregular and granular, and, as a rule, to rise but little above the columella-tangle. The fossa is consequently shallow. Further, the skeleton has always naturally to pass through a stage when it is small and incomplete, as compared with its secreting polyp, which rises in a column above it. Arrest at such a stage would account for the polyp in *Porites* rising high above its shallow calicle.

Lastly, this argument is quite in keeping with the tendency to bud very early, which I have already noted as characteristic of recent Madreporidæ*. The conditions in *Porites* are simply explained if we assume them to have acquired the habit of budding still earlier, *i. e.* when the skeleton is quite immature.

So far, then, as the genus *Porites*, with its minute polyps and feebly-developed skeletons, is concerned, the above arguments appear to me to be fairly conclusive as to their relationship with some primitive Madreporidæ as fixed young forms.

The chief qualification of this conclusion would tend towards suggesting a polyphyletic origin to *Porites*. There is no reason to suppose that this arrest of development happened only once. If it is possible at all, it is likely to have taken place more than once and at different stages in the phylogenetic development of the Madreporidæ. Indeed, we might ask whether it is absolutely necessary to assume an exclusively Madreporid origin. These points must be left for future discussion. They require a much wider survey of forms than we now possess, and a more profound insight into the essential morphology of the Madreporarian groups.

The genus *Goniopora*, Q. & G.—The first known forms of this genus led to their being placed near, and even among, the Astræidæ (Milne-Edwards & Haime). These last-named authors kept the name *Goniopora* for forms with thick-walled, rather shallow calicles, but gave the name *Porastræa* to those with thin walls. This latter name explains itself. Dana first placed the genus with *Porites*, with which it agrees in almost every respect except in size of calicles. The only difference I have myself been able to discover can be referred simply to increased growth. A third cycle of septa appears, which may be merely rudimentary,

* Brit. Mus. Madrep. vol. iii. p. 12.

but is most often well developed and with a fourth cycle indicated. The lamellate character of the septa is more evident in the larger septa of *Goniopora* than in the smaller septa of *Porites*, the perforations being about the same size. Thus the perforations as such are of less account in *Goniopora* than in *Porites*, and the vertical section is more of an irregular reticulum than a regular lattice-work, as it frequently is in *Porites*. The close relationship between *Porites* and *Goniopora* suggested by Dana has been universally accepted, Milne-Edwards and Haime abandoning their former position as soon as possible after Dana's work appeared. There has, however, been a tendency to limit the genus too much to forms which have tall thin walls and consequently deep calices. As a matter of fact, the range of variation is very great; and the collection in the Natural History Museum contains many new and beautiful forms.

Admitting this genus, then, as a near ally of *Porites*, the much greater size of its calices raises an objection to our conclusions. *Porites*, by the small size of its calices, might easily be accounted for in the way above suggested as fixed young forms. But how shall we explain the much larger size of the calices of many Goniopores?

It seems to me that these need not present any great difficulty. Passing over the possibility above suggested, that in these Poritidæ we may have a group made up of fixed young forms of several different corals, whose separate ancestries it would now be extremely difficult to unravel*, there need be no difficulty in deducing the Goniopores from *Porites* directly; and this seems, for the practical purposes of classification, the simplest course to pursue, provided, however, we do not lose sight of the above-mentioned possible polyphyletic origin.

I propose, then, to regard the Goniopores as merely enlarged *Porites*, a kind of giant race which retains the skeletal habit of *Porites*. If once that habit became fixed, there is no reason why further growth should not simply enlarge it without necessarily running it into ancestral Madreporidan lines.

In the present state of our knowledge, I regard anything like certainty in these relationships as unattainable. What I have

* Here it is of great interest to note that Dana himself suggested that *Goniopora* might occupy a position in the Caryophyllacea corresponding to that which *Porites* occupies in the Madreporacea (Zoophytes, p. 407).

here sketched out is intended to serve merely as a working hypothesis. It may be that a closer study of fossil forms will reveal to us new possibilities. In the meantime, however, we have to analyse the structures of the forms which we have at our disposal, and to arrange them as best we can in a natural order.

Several other genera, recent and fossil, were boldly classed among the Poritidæ by Milne-Edwards and Haime. Any corals showing the "trabecular" structure were placed in the family, which was divided into two subfamilies, *Poritinæ* and *Montiporinæ*.

The *Poritinæ* contained the genera *Porites*, *Rhodaræa*, *Goniopora*, *Litharæa* (foss.), *Protaræa* (foss.), *Alveopora*, *Microsolena* (foss.), *Mæandraræa* (foss.), *Coscinaræa*. In addition to these, *Porites* was divided by Verrill into *Porites* and *Synaræa*; by Duchassaing and Michelotti into *Porites*, *Neoporites*, with a new genus *Cosmoporites*; while Quelch added another, *Napopora*, and described a new genus, *Tichopora*, as closely allied to *Rhodaræa* and *Goniopora*.

Any adequate discussion of these genera should be preceded by a detailed anatomical account of *Porites* and *Goniopora*, showing their ranges of variation. Such an account is in course of preparation. But in the meantime enough has already been said to make the following short notes on the claims of the various genera to a place in the family intelligible. Further, of these genera I propose only to refer to those which I know at first hand. I am not sufficiently acquainted with the fossil forms (which require a much closer study than I have yet been able to give to them) to desire to offer any opinion as to their claims to a place in the family.

Synaræa, Verrill.—This genus was separated from *Porites* by Dr. Verrill*, on the suggestion of Milne-Edwards and Haime, to contain certain forms in which the calicles are quite filled up by the intercalicular skeleton, *i. e.* which show a mere variation in the depth of the calicle. My own study of the variations in *Porites* makes it doubtful whether this is always even a specific, much less a generic distinction.

Napopora, Quelch.—In the genus *Porites* there exist species

* Bull. Mus. Comp. Zool. vol. i. (1854) p. 42.

in which the thickened walls show tendencies to form extra ridges and hillocks closely resembling those of *Montipora*: indeed, but for the calicles, such specimens would certainly be classed in that genus. These were not known when Quelch made his new genus*. There are, however, a good many in the British Museum collection. It seems to me as impossible to separate them from *Porites* because of this rising of the wall, as it is to separate *Synaræa* on account of the sinking of the wall. *If the calicles are built on the same plan*, variations in height of the wall can hardly be considered as generic distinctions.

Both these genera therefore, *Synaræa* and *Napopora*, are merged in the genus *Porites*.

Rhodaræa.—This genus was established by Milne-Edwards and Haime †, and was thought to differ from *Goniopora* in that the latter had tall thin walls and spongy columella, while *Rhodaræa* had thick low walls with a rosette of pali rising off the columella. These differences are only slight variations on the same essential structure. Even in individual stocks, the development of the pali is always the inverse of that of the walls; where walls are low, the pali are high and conspicuous. In any extended survey, it is found absolutely impossible to separate the specimens on these lines. I propose therefore to merge this genus into *Goniopora*.

Tichopora, Quelch ‡.—The union of *Goniopora* and *Rhodaræa* forms a group which absorbs this proposed genus, in that it came somewhere between them, differing but slightly from either.

Alveopora.—This genus was the subject of my former paper (*l. c.*), so that I need only repeat the conclusion at which I have arrived, that, in spite of its occasional resemblance to individual forms of *Goniopora*, as a primitive type of coral it is yet very far removed from the Poritidæ, which must rank among the most specialized of the Madreporaria.

Coscinaræa, M.-E. & H.—Very little is known of this genus. Only one species seems to be known. It was first figured in Savigny's 'Descr. de l'Égypte,' pl. v. fig. 4, 1809, and named *Meandrina*. These are very puzzling figures, and hardly suggest

* Ann. & Mag. Nat. Hist. xiii. (1883) p. 296.

† C. R. xxix. p. 259 (1849).

‡ Chall. Rep. xvi. (1886) p. 188.

any affinity with *Porites*. A second figure, however, is given, evidently of another specimen, by Milne-Edwards and Haime (Ann. d. Sci. Nat. 3 ser. ix. pl. v. fig. 2, 1848). This was first named *Coscinaræa Bottæ*, M.-E. & H., but afterwards, being identified with Savigny's figure, became *Coscinaræa meandrina*. Dr. Klunzinger has fortunately re-discovered and photographed it as *Coscinaræa monile* of Forskål, and regards it as a Fungid*.

The remaining subfamily of the Poritidæ, M.-E. & H.—the *Montiporinæ*—consisted of two genera, *Montipora* and *Psammocora*, Dana.

Montipora.—This genus is one of those which Milne-Edwards and Haime forced among the Poritidæ solely on account of its “trabecular” septa. I have already analysed the skeleton of *Montipora* and compared it with that of *Porites* †. I was, however, all the while conscious of some misunderstanding; the confusion lay in the word “trabecula.” I endeavoured to show that the trabeculæ of *Porites* were not the same as the vertical rods which form such a conspicuous element in most sections of *Montipora*, the secondary development of which could be traced within the genus. I am now, however, not satisfied that Milne-Edwards and Haime meant these vertical rods at all. The word “trabecula” must have meant for them both vertical and horizontal rod-like skeletal processes; and the trabeculæ of *Montipora* were, for them partly at least, the short blunt septal teeth, and not exclusively the long nodulated rods which, in the sections of some forms, so closely resemble the vertical rods in sections of *Porites*. Their express words, in discussing the claims of *Montipora* and *Psammocora* to be classed among the Poritidæ, are: “La structure trabiculaire de leur polypier et principalement de leurs cloisons ne peut laisser aucun doute sur leurs véritables affinités” ‡. Further, their description of the septal apparatus of *Alveopora* as “trabecular” leaves little doubt that in their use of the word they meant either vertical or horizontal rod-like skeletal matter.

It is not surprising, therefore, if the word “trabecula” (“poutrelle”) has caused confusion, for this indefinite application of

* ‘Corallenthiere,’ iii. 1879, p. 78.

† Ann. & Mag. Nat. Hist. xx. 1897; cf. also Introd. vol. iii. Brit. Mus. Mus.

‡ Ann. Sci. Nat. 3 ser. xvi. p. 54 (1851).

the term is quite inconsistent with the original description, where the trabeculæ are said to have "l'aspect de petites tiges noueuses, étranglées d'espace en espace"*. The septal teeth of *Montipora* do not conform to this description, while the vertical rods in that same genus and in *Porites*, as a rule, do.

For the future, however, the word "trabecula" represents merely so much formative tissue, and, if it and its adjectives are retained at all, they can only have descriptive significance. Their intrusion into the morphology of the Madreporaria has so far only led to confusion. I must again, therefore, express my conviction that the more exact description of the trabecula given us by Miss Ogilvie is solely of histological importance, and cannot again give it any weight as a morphological unit.

Returning, however, to the genus *Montipora*, my researches have led me fully to endorse the widespread opinion that it belonged to the Madreporidæ, and not to the Poritidæ. A comparative study of their skeletons showed them, as I thought, to be quite distinct. It is therefore not without interest to note that the conclusion we have now arrived at as to the origin of *Porites* has once more brought them in a manner together. Both may be called Madreporids in which the polyps are fixed at a very low stage of development, but the processes in the two cases are in strange contrast. In *Porites* the whole organization, polyp and skeleton, never gets beyond the early stage at which their development is arrested. But, in *Montipora*, the dwarfing of the polyps seems to have been due to the excessive development of the skeleton as such. The Madreporarian skeleton, in fact, reaches its highest level of specialization in this genus, though at the expense of the polyps. The dwarfing of the polyps in the two genera gave some colour to the classification which placed them in the same family. Indeed, forms occur in both genera which it is not easy at first sight to assign to the one or to the other. Milne-Edwards's distinction, that one has an interstitial cœnenchyma and the other has not, does not hold good, for there are many *Porites* with such thick walls that no difference in this respect can be recognized. The real distinction is found in the calicles. The septa of *Montipora*, composed of six vertical rows of small horizontal teeth round a deep fossa, are unknown

* 'Les Coralliaires,' vol. i. (1857) p. 32.

in *Porites*; while, on the other hand, the columella-tangle with the paliform granules or rods rising from it, which are characteristic of *Porites*, are never seen in *Montipora*.

Psammodora, Dana, is the last genus which Milne-Edwards and Haime placed in their Montiporine subfamily of the Poritidæ. Dana, from a study of the living coral and on account of its skeletal structure, placed it among the Fungidæ. Its "trabecular" structure, however, compelled Milne-Edwards and Haime to transplant it. So far as I can see, beyond the granular interrupted edges of the septa, which thus appear to be built up of "trabeculæ," this genus has no claim whatever to be classed anywhere near *Porites*, and I agree with Dr. Klunzinger, who replaces it among the Fungidæ, in removing it from the Poritidæ.

Neoporites and *Cosmoporites*, Duchassaing and Michelotti*.—We can discuss these suggested genera together: the differences between them are slight, and the real question is whether they should be separated from *Porites* at all. The type of the suggested *Neoporites* may be taken to be the West-Indian *Porites astræoides*, Lamarck, which, with a few other West-Indian forms, differs from all the recorded *Porites* in having deeper calicles and either no pali or else mere traces of them ("pallulis nullis vel subevanidis"). This absence of pali and greater depth of fossa are certainly remarkable characteristics. But I find myself compelled to agree with Dr. Brüggemann in claiming them to be true *Porites*. On the one hand, it may be urged that the pali are an essential characteristic of *Porites* and *Goniorpora*; and here we have forms in which the pali have been secondarily obscured or even suppressed; hence the need for establishing a new genus, and if so the name *Neoporites* is most felicitous, because it betokens an advance on the main genus; further, all the forms which might be grouped as *Neoporites*, and which have been so far described, occur in the West Indies, *i. e.* they have a certain geographical unity which greatly supports the structural evidence in favour of their being a new generic development. On the other hand, I would suggest that, if these specimens are removed from *Porites* on account of the absence of pali, they should for the same

* 'Coralliaires des Antilles,' Suppl. 1864.

reason be removed from the family. Further, a review of the structural variations not only within the genus, but even often on one and the same specimen, reveals a correlation between the wall and the pali, so that when the one is specially well developed the other is correspondingly aborted. In *Goniopora* we have the species *G. Stokesi*, in which the walls are high and the pali are either absent or else only hinted at. And lastly, forms occur, and will shortly be described, in the Indo-Pacific area which show this same variation, viz., absence of pali. There seems to me, then, no special advantage in separating a few specimens of *Porites* because the deepening calicles have led to the partial or complete suppression of the pali. This variation seems to me not too great to be comprised within the range embraced by the genus.

In connection with what has been said above about the relation of *Porites* to the Madreporidæ, the resemblance between these "*Neoporites*" of Duchassaing and Michelotti, in which the pali are absent from the deep central calicles, and *Montipora* is very interesting: it shows how along two different lines almost the same structure may be reached. That these forms are not Montiporids may be gathered—(1) from their habit, which is more like that of *Porites* than of *Montipora*; (2) from the walls being more boldly reticular than in the majority of Montipores; (3) in the presence of a columella-tangle slowly filling up the fossa, this being characteristic of the Poritidæ but not of the Madreporidæ (excl. *Turbinaria*); (4) in the traces of pali in the shallower young calicles; (5) in the twelve septa nearly equal in size, whereas in *Montipora* six, with a rudimentary second cycle, is the usual septal formula.

SUMMARY.

The foregoing pages contain a preliminary instalment to a revision of the classification of the Madreporaria by Milne-Edwards and Haime, which has been rendered necessary by recent advances in our knowledge of the morphology of the coral-skeleton.

The object of the paper is to record the results, obtained during my work of cataloguing the specimens in the Natural History Museum, as to the position of *Porites* among the Madreporaria. A brief sketch of the history of the question

led to a review of the present situation, in which the fundamental theory on which the existing system of classification which we owe to Milne-Edwards and Haime rests was criticised in the light of recent research. This criticism entailed a re-statement, with slight amplification, of the author's phylogenetic scheme, along the lines of which it is maintained the classification of the Stony Corals will have, for the future, to proceed, *i. e.* until it is again superseded by further advances in morphological science. The chief new points of interest with regard to this scheme related, (1) to the origin of septa; (2) to the various possible methods in which the primitive external epithelial cup may have been flattened and become replaced by an internal skeleton.

This last discussion brought us naturally to the object of the paper, *viz.*, to enquire along what lines of development *Porites* obtained its peculiar internal and so-called "trabecular" skeleton.

The conclusions arrived at were:—

(1) The "trabecular" septum is only a misleading name for perforated lamellate septum.

(2) The Poritid skeleton can be explained as an immature Madreporid skeleton, arrested in its growth by very early budding.

(3) As this may have happened more than once, *Porites* may be polyphyletic in origin.

The paper concludes with a brief discussion of the various genera which have been from time to time united with *Porites* in the same family or else separated from it as generically distinct. The revision suggested leaves the family Poritidæ as Dana left it, with only two genera, *Porites* and *Goniopora*,—*Porites* enlarged by the absorption of *Synaræa*, *Napopora*, *Neoporites*, and *Cosmoporites*, and *Goniopora* also enlarged by the merging with it of *Rhodaræa* and *Tichopora*.

My best thanks are due to my friend Prof. F. Jeffrey Bell for much kindly assistance, and for the warm interest he has taken in these investigations, not only as the Officer in charge of the Collections on the study of which they are based, but also in the interest of zoological science.
